On Some Gastrocotyline (Monogenoidean) Parasites of Indian Clupeoid Fishes, Including Three New Genera

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ABSTRACT: Seven species of monogenetic trematodes, including the two genotypes, *Engraulicola forcepopenis* George, 1961 and *Engrauliscobina thrissocles* (Tripathi, 1959), are recorded. All seven of these atypical gastrocotylines belong to the subfamily Gastrocotylinae s.s. and are parasitic on clupeoid fishes. Four species in the present collection, viz., *Engraulicola micropharyngella* sp. n., *Engraulixenus malabaricus* gen. et sp. n., *Engrauliphila grex* gen. et sp. n., and *Engrauliscobina triaptella* sp. n., were collected from fishes of the family Engraulidae, while an entirely new type, *Pellonicola elongata* gen. et sp. n., was obtained from Clupeidae. The tendency to unilateral inhibition of the clamp rows is incomplete in all these atypical gastrocotylines, and all are characterised primarily by their clamp structure. Diagnostic characters, with special reference to the haptor (its adhesive units or clamps and anchors), the male terminalia, vaginal complex, and other salient features which appear to be taxonomically important, are given for each species.

Some gastrocotylid worms have been found on the gills of clupeoid fishes at Mandapam Camp. Their clamp structure shows them to be allied to *Gastrocotyle* and *Pseudaxine*. The tendency to develop a unilateral haptor is another common feature. But of the 32 known species of Gastrocotylidae, and 8 new species described by me (in press), all 40 are parasitic on scombroid fishes (including Carangidae). Indeed, it is usual to find these more highly evolved Monogenoidea on the more highly evolved fishes, while the simpler clupeoids are typically parasitized by Mazocraeidae. The occasional excursions across the phylogenetic trees of the hosts for each of these families of parasites have been discussed by Sproston (in press). The present collection adds support to her hypothesis, since it contains four new forms from Engraulidae and one entirely new type from Clupeidae. Collection and treatment of specimens was performed as described in a previous paper (Unnithan, 1957:28–29).

All of these atypical clupeoid parasites belong to the subfamily Gastrocotylinae *sensu stricto,* hitherto containing only *Gastrocotyle* v. Ben. et Hesse, 1863, *Chauhanea* Ramalingam, 1953, and *Yamaguticotyla* Price, 1959. They are characterized primarily by their clamp structure (Unnithan, 1967*b*). There are paired braces in the posterior region of the clamp capsule, as in all Gastrocotyloidea (as distinct from Microcotyloidea), but the clamps themselves are bilaterally symmetrical; and, unlike the subfamily Priceinae, for instance, to which *Pseudaxine* belongs, there are no complex dorsal shields to other sclerites developed in the dorsal wall of the capsule in association with the median spring, nor are there riblike thickenings in the capsule walls. While in *Gastrocotyle* spp. the ventral arm of the spring is often doubly bifid, its ends sometimes form articulated struts to the jaw rami. This condition is not found in the other genera. In all of them (with the doubtful exception of *Chauhanea* and *Yamaguticotyla*), the dorsal arm of the spring bears a forked appendix associated with noncuticularized ligaments, presumably a transitional condition to that in Priceinae.

The tendency to unilateral inhibition of the clamp rows is complete in *Gastrocotyle* spp. (also in *Pseudaxine* in Priceinae and in some

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Axinidae), but it is incomplete in all the atypical clupeoid parasites described in the present study.

The partition of genera is based on criteria which have appeared to be valid for genera of other subfamilies of the higher Monogenoidea, namely:

(1) The relative encroachment of the clamp rows up the body proper (as distinct from a tail-like haptor quite distinct from the body, for example in *Chauhanea*), which determines the *zone of pivoting* in all the possible feeding attitudes of the attached worm. If this pivoting zone occurs in the thicker gonad zones, then the torque set up will tend to a somatic asymmetry (e.g., *Engrauliscobina*); if, on the other hand, it is near or beyond the end of the testes zone (as in *Engraulicola, Pellonicola,* and *Pseudaxine*), then the highly contractile body may be irregular in outline at any one moment, but very little permanent strain would be registered, and there is no structural asymmetry in the body proper. Nor is this asymmetry present in forms where the pivoting zone occurs anterior to the gonad zone: the forebody alone in these forms is free to bend, and again no true somatic asymmetry is developed (e.g., *Gastrocotyle, Engraulixenus,* and *Engrauliphila*).

(2) The degree of suppression of one side of the haptor. It is considered that there is a greater difference between complete suppression and the inhibition of all but one, or of all but two or three clamps, than between inhibition of only about half the clamps.

(3) The form of the anchors, as has been shown by Llewellyn (1957: Figs. 22 and 23 for *Gastrocotyle* and *Pseudaxine,* and similarly in 1959: Figs. 8 and 9), is regarded as a generic character. The useful differences are the relative lengths of the handle (main root) and hook, of the spur (secondary root), and the approximate segment of a circle represented by the sickle-like hook. These characters are fundamental, since they are developed in the postlarval stages of the onomiracidium, and persist throughout life unless anchors are shed. The persistence of other larval anchors may be a specific character.

(4) Additional sclerites associated with the penis, e.g., the peculiar forceps on the penis head. The only possible analogue is found in *Heterapta* Unnithan, 1961 (Heteromicrocotylidae), where the two spines appear to have a much deeper origin and are straight and much longer, probably functioning as vagino-dilators.

(5) The occurrence of a single median dorsal vagina, or of paired vaginae opening laterally, at various levels, and their separate confluence into the lateral vitelline ducts, or the intervention of a median duct and, in some cases, the direct course of this to the oötype (as is more usual with an unpaired vagina).

(6) The relative size of the oral pouches and the pharynx (expressed as percentage of mean diameters), and the absolute size range of the latter and its shape.

In view of the possibility of a wide array of related forms being discovered on tropical clupeoids in the future, I hesitate to give formal generic and specific definitions for these new forms, but prefer rather to list their diagnostic characters, with particular reference to the six criteria listed above, and other salient characters which appear taxonomically important in each case.

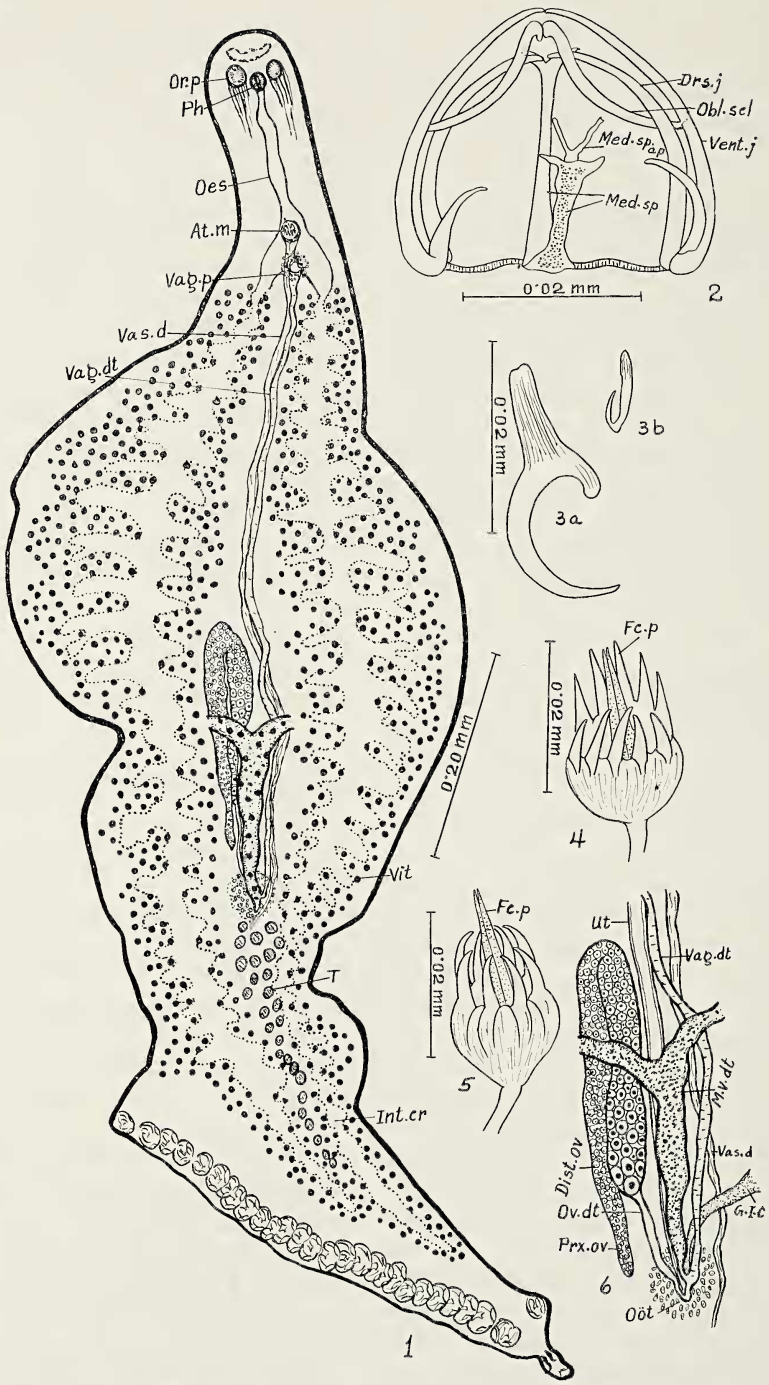
Engraulicola micropharyngella sp. nov.

Figs. 1–6

Four specimens of this new gastrocotyline were collected from the gills of two mature female *Anchoviella commersonii* (Làcepé.) examined at Trivandrum on August 14, 1957. All of the specimens except the one whole mount figured were broken while staining. The description is based mainly on this well prepared specimen (Fig. 1), but comparative measurements on the broken ones are also included.

Body proper essentially bilaterally symmetrical, anterior and posterior ends narrower; "neck" long and slender, about one-sixth of the total worm; haptor triangular with a short terminal lappet (Fig. 1). Total length 1.3–1.9 mm and maximum width 0.42–0.64 mm immediately in front of the ovary.

Mouth subterminal and crescentic; oral pouches thin-walled, spherical, 16–20 μ in diameter, opening into the buccal cavity; pharynx (unusually) smaller than oral pouches, spherical and thin-walled, 14 μ in diameter (ratio of oral pouch to pharynx = 130%); oesophagus



FIGS. 1–6. *Engraulicola microphary ngella* sp. nov. *1*, Complete worm, dorsal view; *2*, clamp, dorsal view; *3a* and *3b*, proximal and distal anchors; *4*, penis with the corona of spines and the forcepiform process; *5*, penis of another specimen; *6*, oötype and ovarian region, dorsal view.

long, narrow, unbranched, and bifurcating into the intestinal crura at the level of the male genital pore; crura with long irregular outer and short simple inner branches; both crura extend into the haptor and terminate at different levels, one extending farther than the other. In the haptoral region the crura are unbranched and the ends are not confluent.

In the specimen examined the haptor bears a long row of 27 clamps on one side, and a single clamp on the other. It is inclined to the body axis at 45°–60°, and is about 35% of the body length. All the clamps are of the same structure, though they vary in size from 16 × 20 μ to 28 × 40 μ. The anteriormost clamp of the long (left) row is the smallest and the single clamp on the right side is more or less of the same size. It is reasonable to expect amphitypy, the long uninhibited row being on the left or right according to the location of the worm on the gill; further collection may show this relationship.

Clamps typically gastrocotyloid in structure: dorsal arm of median spring short and narrow with a thin V-shaped cuticular projection from its distal end; ventral arm of median spring long and narrow, distally bifurcated; base of clamp with a thin, narrow, heavily cuticularized hinge ligament on each side, connecting the median spring with the base or region of articulation of the jaw sclerites; dorsal and ventral jaw sclerites of the two sides symmetrical; dorsal arm of ventral jaw reaches to the level of the bifurcation of the dorsal arm of the median spring; oblique sclerites ("braces") long and narrow, with their distal ends touching in the median line, where their backwardly bent tips form an articulating surface, just within the dorsal jaw (Fig. 2).

Terminal lappet small and cylindrical, 21 μ broad and 36 μ long, demarcated from the rest of the haptor by a small constriction and armed with two pairs of symmetrically placed anchors: anterior pair typically sickle-shaped, 24 μ long, the hook being about three-eighths of a circle. The spur root is short and bent posteriorly toward the point of the sickle, while the handle is less than half the total length (75% of the sickle) (Fig. 3a). It is interesting to note that the spur pointing posteriorly toward the point is also characteristic of the large anchor of *Gastrocotyle* (Llewellyn, 1957: Figs. 12 and 22). The posterior pair is exceptionally small, with sharply reflexed hooked ends; their overall length is 8 μ (Fig. 3b).

The testes are all postovarian; there are about 27 small spheroidal follicles in 2–3 irregular files extending more or less to the hind end of the shorter intestinal crus or halfway down the haptor. The vas deferens runs forward, curving to the right around the ovarian zone beyond which it becomes median and opens into the base of the penis, apparently without a vesicular dilatation. The atrium masculinus is in the zone of the intestinal bifurcation. The cuplike penis has a thick muscular wall, its rim armed with a corona of 8–10 hooked spines with their tips converging. From the centre of the penis cup on the penis head is a forceps-like, lightly cuticularized structure 13–16 μ long, much longer than the penis hooks, and projecting slightly beyond the penis corona (Figs. 4 and 5). No collar was seen like that described by George (1961) for the genotype.

The ovary is an inverted U, its field 210 × 63 μ, situated in front of the testes; its outer longer limb is narrow and the distal inner limb is thicker and contains larger ova. The oviduct arises from the distal end of the ovary, runs backward, and opens into the oötype through a short narrow basal loop (Fig. 6); the uterus arises from the oötype close to the oviduct, runs forward along the median line, and opens near the male genital opening. Eggs spindle-shaped, 40 × 24 μ.

Vitellaria massive, extending from the level of intestinal bifurcation to the tips of each intestinal crus and covering the crural branches, not confluent across the median line; vitelline follicles spherical, 8–10 μ in diameter. The transverse vitelline duct lies at the level of the first third of the ovarian zone, and the median vitelline duct tapers slowly until it reaches the oötype.

The oötype is surrounded by few scattered Mehlis gland cells. The genito-intestinal canal curves toward the right side and opens into the right crus in the midoviduct zone.

The median dorsal vagina is unarmed and is situated in the angle of the intestinal bifurcation, *immediately behind* the muscular unarmed rim of the atrium masculinus and sur-

rounded by small spherical gland cells. The vaginal duct is narrow and runs backward dorsally along the median line parallel to the vas deferens and opens into the vitelline ampulla, independently of the vitelline duct (Fig. 6).

RELATIONSHIPS OF *Engraulicola micropharyngella* SP. NOV.:[2]

1. *Engraulicola* is characterized by the general shape of the body, which resembles a "treed" riding boot, the handle of the boot tree being represented by the slender neck, the main clamp row the sole of the boot (with the metahaptor as the heel), and with the single clamp of the inhibited row suggesting the toe cap of the boot. In other genera a toelike projection is not developed.

i. In *E. forcepopenis* George, 1961 the foot and toe are nearly at right angles to the body proper and the testes scarcely enter the foot, the zone of pivoting being behind the testis zone. In *E. micropharyngella* sp. nov. the foot is more tapered to the toe and is only 45°–60° to the body axis, and anteriorly a few single-file testes enter the foot and are included in the zone of pivoting. The heel is a little thicker, but no haptoral wing with special gut branches is developed.

ii. The haptor is less than 50% of the axial length in the genotype, but only about 35% in the new species.

2. In the three larger individuals of *E. forcepopenis* bearing shelled eggs, the haptoral fringe had 44, 39, and 33 clamps, and the two smaller individuals (total length 1.3–1.5 mm) had only 21 and 25 clamps. In the unbroken specimen of *E. micropharyngella* (1.3 mm long), there were 27 clamps; the broken individuals (1.4–1.8 mm long) had 28, 29, and 32 clamps. In all individuals of both species there is a single clamp on the toe cap.

i. The clamp is wider than long in the former species (length/width = 55–60%), and in the latter is relatively not quite so wide (70%). In both, the solitary clamp is nearly as long as wide, but smaller than those of the other side. The mean diagonal of the solitary clamp in the genotype is 33.2 μ (calculated from the *mean* of the square root of the product of diameters, $\sqrt{l \times w}$), and that of the new species is only 18 μ, i.e., about 54% of the size of the single clamp in the genotype.

ii. The appendix of the dorsal arm of the median spring in *E. forcepopenis* is shown as Y-shaped with a short stem. In the present one it is V-shaped with a minute base only, and the posterior ends of the braces are bent back as opposable knobs.

3. Of the two pairs of persistent anchors, the anterior is typically sickle-shaped in both; in *E. forcepopenis* the sickle is about half a circle and the hook nearly equal, but in *E. micropharyngella* the sickle is only about three-eighths of a circle and the length of the handle is only about 75% that of the sickle. The total length of the anterior anchors in the former is 29 μ, and 24 μ in the latter. The posterior simple, hooked anchors are much smaller in the new species (13.6 μ and 8 μ, respectively).

4. The forceps on the penis head are practically identical in both form and size, but the collar observed in the genotype, projecting ventrally from the atrium masculinus, has not been seen in the present material, where the rim of the atrium is a simple flat muscular ring.

i. In *E. forcepopenis,* though it is larger, there are barely half the number of testicular follicles that are present in the new species. *E. micropharyngella* has no parovarian follicles, while one or two are found in *E. forcepopenis.*

ii. The spines of the genital corona of *E. forcepopenis* are invariably 12, but only 8–10 are present in *E. micropharyngella.*

5. While both species have a single median vagina with a duct direct to the oötype, in *E. forcepopenis* the vulva is halfway between the male genital pore and the vitelline ducts, and in *E. micropharyngella* it is strikingly farther forward, lying immediately behind the male genital pore.

[2] Generic characters are indicated by Arabic numerals, specific characters by small Roman numerals.

6. The relative size of oral pouches (mean diagonal from $\sqrt{l \times w}$) and pharynx in the genotype is 50–77%, the pharynx as usual being ovoid and larger than the ovoid oral pouches. But in *E. micropharyngella,* while the oral pouches are nearly round the ovoid pharynx is minute, the former 130% of the latter. Hence this most obvious specific character is indicated in the name.

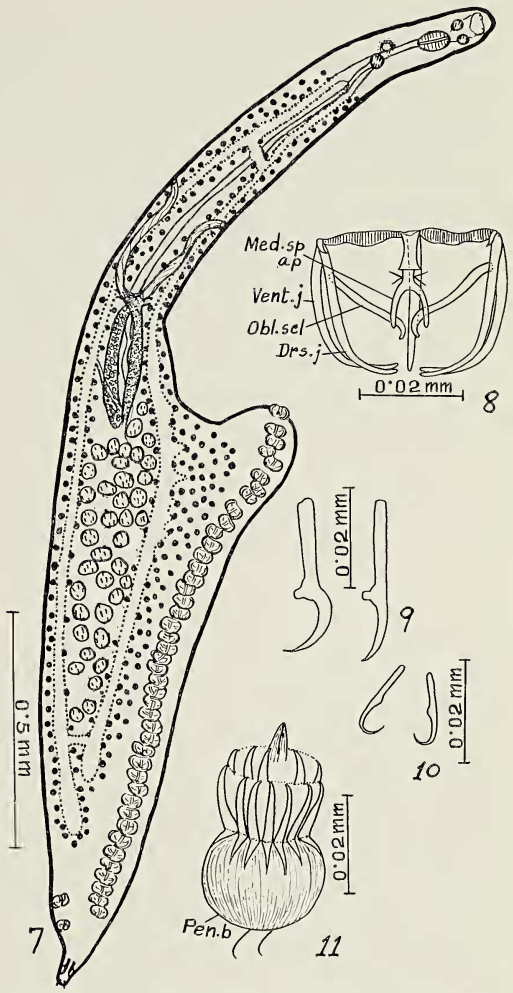
In view of these important characters I agree with George (1961) in his creation of *Engraulicola,* with *E. forcepopenis* as the type. The above description was written before the paper by K. C. George was available to me, but we had previously agreed on the nomenclature of his material (described some years earlier than mine) from the same geographical region (South Malabar coast).

Engraulixenus malabaricus gen. et sp. nov.
Figs. 7–11

Several specimens of this new species of engraulid parasite were obtained from the gills of *Thrissocles malabaricus* (Bloch) examined at Trivandrum on July 26, 1955. Four fishes were examined and all were infected by the new parasite as well as by a large number of two different species of Mazocraeidae. Out of the 52 Monogenoidea obtained, 8 specimens belonged to the present species.

This worm is foot-shaped, with a distinct heel and a long slender forebody, the total length being 1.71–2.43 mm and the maximum width 0.45–0.5 mm (Fig. 7).

Mouth subterminal, without especially glandular or muscular lips; oral pouches spherical, 24–28 μ in diameter; pharynx median, very large, elongated ovoid, 64 × 36 μ–80 × 38 μ; oral pouches not more than 40% of pharynx (by mean diagonals); oesophagus narrow, 0.13–0.19 mm long, bifurcating into the intestinal crura behind the male genital pore; crura exceptional, with 2–3 cross connections bridging across the median line and without much outer branching, the dilated ends (unbranched in posterior third) extending to different levels. At the anterior region of the long clamp row, the crus of that side has a few wider lateral branches, forming the base of what is probably a metahaptoral wing. An oblique connection also occurs between the distal ends of the crura, behind the testes zone, in most of the specimens (Fig. 7).



FIGS. 7–11. *Engraulixenus malabaricus* gen. et sp. nov. 7, Complete worm, ventral view; *8,* clamp of the long row, dorsal view; *9,* proximal anchors; *10,* distal anchors; *11,* penis with the corona of hooks and forcepiform process.

The haptor occupies about 50% of the total length; a fleshy flange adherent to the body (yet with an increasing tendency to diverge from it) forms the wing referred to above. The long clamp row has 42–49 clamps, each 32 × 48 μ–32 × 66 μ; the short row has two nearly sessile clamps 24 × 28 μ, and 28 × 36 μ; lappet 64 × 28 μ, armed with two pairs of anchors. The anterior pair (Fig. 9), 32 μ long, have a shape different from that in *Gas-*

trocotyle and *Engraulicola*: the hook is barely a quarter of a circle, with the handle considerably longer, while the stout spur is at right angles to the handle. The posterior anchors (Fig. 10) are also unusual in having an incipient spur behind the short hook; the total length of these anchors is 16 μ.

The clamp structure shows slight variations from that of *Engraulicola*: there is a marked gradation of size toward the middle of the long row. The clamps are much wider than long, except for the first and next anterior clamps, which, like the two remnant primaries of the inhibited side, are more nearly squarish (Fig. 8).

The 20–39 testes are oval, 28 × 40 μ–36 × 48 μ, arranged in 4–5 files in the intercrural field behind the ovary but with a few parovarian testes on the left side. The narrow vas deferens arises from the postovarian testes, extends forward on the left side of the body, parallel to the vitelline duct and enlarges into a seminal vesicle near the anterior end of the median vitelline duct. From the anterior margin of the seminal vesicle, the vas deferens continues forward and opens into the base of the penis, some distance anterior to the intestinal bifurcation. The penis is muscular and armed with a corona of 12 recurved hooks around its bulb-like base, and there is a forceps-like double spine within (Fig. 11). The forceps spines appear rather shorter than in *Engraulicola.* Male genital pore is strengthened by a rim of radial muscle fibres but is without a projecting collar, and is situated at about 0.27 mm from the anterior end of the body.

The inverted ∪-shaped ovary occupies a field in the middle of the body's length and it is about one-tenth as long as the latter, the ova as usual becoming bigger toward the oviduct. The oviduct arises from the distal end of the ovary and enlarges into a small sphincter-like ovijector which continues through the oötype region and opens into the fertilization chamber near the vitelline ampulla. The uterus can be traced forward from the anterior margin of the oötype, parallel to the vas deferens, and it opens into the unarmed uterine pore situated immediately in front of the male pore.

The paired vaginal pores are unarmed and submarginal and lie in front of the ovarian zone at two-thirds the distance from the male terminalia to the anterior end of the ovary. The vaginal ducts are S-shaped and in the specimens examined were distended with sperm; they run backward and unite in the zone of transverse vitelline ducts to enter the wide median vitelline duct which extends backward, narrows posteriorly, and opens into the oötype, in the small vitelline ampulla. Thus, there is no true median vaginal duct.

The vitellaria extend from the region of intestinal bifurcation to the distal ends of the crura and are not confluent across the median line even in the region of the crural bridges; the spherical follicles are 8–12 μ in diameter. The transverse vitelline ducts meet along with the lateral vaginal ducts immediately *anterior* to the ovarian zone, to form the median vitelline duct which also functions as a vaginal duct. The genito-intestinal canal connects the base of the oötype with the right intestinal crus, passing sharply obliquely forward across the proximal region of the ovary; its union with the right crus is in the midovarian zone (i.e., more anterior than is usual).

RELATIONSHIPS OF *Engraulixenus malabaricus* GEN. ET SP. NOV.:

1. *Engraulixenus* has an elongated tapering body, slender anteriorly, with a long foot-shaped hindbody tapering backward and which has an unusually prominent heel with a spurlike extension; this region is the typical haptoral wing (perhaps a metahaptor: see Unnithan, 1967*b*), which receives short wide branches from the adjacent intestinal crus which branches more or less profusely in the anterior part of the wing; these gut branches carry with them vitelline follicles. The haptor extends slightly obliquely at only 25° to the body axis for at least 50% of its length; thus the zone of pivoting of the attached worm is between the wide testis zone and the ovarian zone. The torque strains set up have not greatly disturbed the symmetry of the body proper but doubtless account for the haptoral wing and subjacent lateral field. The arc of feeding exploration is evidently extensive because of the slender contractile forebody. Thus, *Engraulixenus* is less symmetrical than *Gastrocotyle*.

2. The inhibited clamp row retains two of its primary clamps in all individuals.

i. The long clamp row in mature worms, 1.7–2.4 mm long, bears 42–49 nearly sessile units, closely set, the posterior edge of one touching the anterior edge of the next one.
ii. The larger clamps are at least as wide as long and are the widest of any described in the present study.
iii. The dorsal appendix on the spring is a stalked stout U-shaped piece with parallel arms not divergent as in most of its relatives.
iv. The ventral arm of the spring is not truly bifurcated and is slender throughout.
v. The braces are bent posteriorly for mutual articulation.

3. Of the two pairs of persistent anchors, the anterior are characteristically shaped, with the handle markedly longer than the hook, which is barely one-quarter of a circle, and with a stepped conical spur at a right angle to the handle. The anterior anchors are more slender and shorter than in *Engraulicola,* and the posterior anchors have hooks which recurve for only one-third the length of the blade, and have an incipient spur and a stout handle. They are just half as long as the anterior pair.

4. The forceps on the penis head are similar to those in *Engraulicola*, but they may be relatively stouter and shorter; there is no collar projecting from the rim of the atrium masculinus.

i. The penis spines are sigmoid and 12 in number.
ii. The 20–39 testes are massive in 4–5 files anteriorly.
iii. A vesicula seminalis is present in front of the ovarian zone.

5. In the paired vaginae the vulvae are supramarginal and the lateral vaginae join the transverse vitelline ducts near their confluence, so that there is no true median vaginal duct.

i. The vulvae are situated at two-thirds the distance from the male genital pore to the anterior end of the ovary. The vitelline ducts are usually long and oblique and they become confluent into the median vitelline duct distinctly *anterior* to the ovarian zone.

6. The pharynx is exceptionally elongated and ovoid, the longest (80 μ) in the whole group; the mean diagonal of the spherical oral pouches is 40% or less that of the pharynx.

7. Exceptional intercrural bridges occur twice or thrice in the forebody, and often in the posttesticular zone there is an oblique bridge. This is the most obvious generic feature, but it is perhaps less important than are the preceding criteria taken together.

i. The ends of the crura are subequal and markedly inflated, the longer being on the inhibited side, and reaching to opposite the sixth or seventh clamp from the posterior end.

The specific name is derived from the host and locality, the South Malabar coast.

Engrauliphila grex gen. et sp. nov.
Figs. 12–17

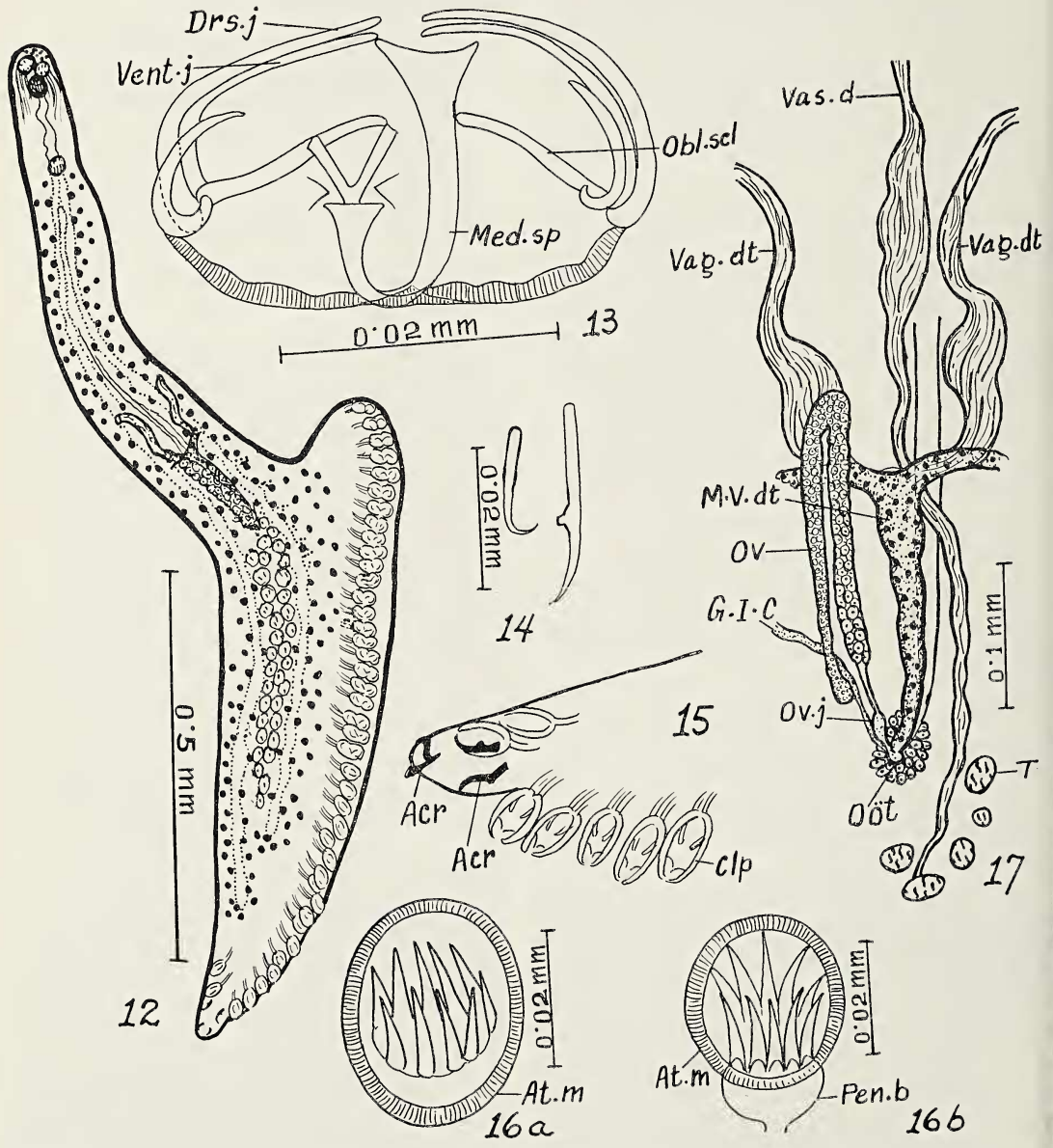
Specimens of this new gastrocotyline genus were found swarming on the gills of *Thrissocles dussumieri* (Val.) examined at the Southern Indian Marine Biological Laboratory at Trivandrum on October 5, 1955 and at Ayirumthengu on September 8, 1955. Those from Trivandrum had a multiple infection including a relative, *Engrauliscobina triaptella* sp. n., while those from Ayiramthengu were infected with the present species only. Numerous specimens were collected from a single fish, a minimum of at least 50 being very common. However, many fishes of the same host species examined at Vizhinjom (another marine biological station, 8 miles south of Trivandrum) on August 19, 1954 were not infected by *E. grex.* There the characteristic parasite was *Engrauliscobina triaptella.*

This worm is foot-shaped with a spurred heel, but the "leg" comprising the anterior half is only about half as wide as the stout hindbody, which tapers evenly to the terminal lappet; total length 1.3–1.8 mm and maximum width 0.25–0.3 mm, including the haptoral wing or spur of the heel (Fig. 12).

The subterminal mouth is wide, with an anterior circlet of scattered sticky cells. The spherical oral pouches are 24–32 μ in diameter, with thin walls but with long muscle fibres extending backward; the relatively long ovoid pharynx is

40 × 60 μ–44 × 72 μ, with thick walls and radial muscle fibres strengthening it; the mean diagonals of the oral pouches are about 50% of the diagonal of the pharynx. The narrow oesophagus is 0.12–0.18 mm long and bifurcates into the intestinal crura just behind the male terminalia. These crura lack both intercrural branches and bridges, and have very few outer branches; they terminate posteriorly at different levels in the posterior third of the hindbody, where their ends are slightly inflated. The crus on the inhibited side of the haptor is the longer, reaching to opposite the fifth clamp or so from the posterior end of the longer row, well in front of the two clamps of its own side.

The intestinal crus on the side of the body



FIGS. 12–17. *Engrauliphila grex* gen. et sp. nov. *12,* Complete worm, ventral view; *13,* clamp, ventral view; *14,* anchors; *15,* hind end of haptor with the anchored lappet; *16a* and *16b,* male genital pore with the armed penis; *17,* öotype and ovarian region, ventral view.

bearing the main row of clamps has more extensive outer branches, particularly in the haptoral wing, which are accompanied by vitellaria. This winglike expansion of the haptor is similar to that in *Engraulicola micropharyngella* described above, but although the present worms are on the whole smaller, the haptor is stouter. All the clamps have relatively long muscular stalks (about as long as the width of the clamps) which project sideways in close file. As in the previous species, the clamps increase in size toward the middle of the row, where there is a slight irregularity. This may indicate the end of the euhaptor and the beginning of the metahaptor, which tends to grow with increasing independence of the body proper, its anterior part being free from it—as the metahaptoral wing (Fig. 12). The long row makes an angle of only about 30° with the body axis. There are always two remnant clamps on the inhibited side, smaller (20 × 28 μ–28 × 36 μ) and resembling their opposite primaries. The long row is more than half the length of the worm, with 40–48 clamps, each 28 × 40 μ–28 × 60 μ.

The terminal lappet is trapezoidal, 0.04 × 0.02 mm, with two pairs of anchors. The anterior anchors are 28 μ long and slender; the hook is less strongly curved (only one-eighth to a quarter of a circle), with a short stepped spur, projecting at right angles at the end of the slender handle which is more than half the total length (Figs. 14 and 15). Thus there is a strong resemblance to the anterior anchors of *Engraulicola micropharyngella*. The posterior anchors generally resemble those of the last species, but the simple hook is barely one-third as long and is less curved (about half a circle), while in the last species the hook was more than half a circle (cf. Figs. 14 and 10).

The clamp structure is quite distinctive in detail (Fig. 13); the larger clamps are as much as twice as wide as they are long. In sharp contrast to the two previous species, the ventral arm of the median spring is broad and widely bifurcated in a thick pointed fork. The dorsal arm carries a V-shaped stout appendix with arms widely diverging. The braces are not bent at the posterior ends to form articulating facets, as in the preceding species.

The testicular zone is entirely flanked by the haptor flange, which extends over the hind end of the ovary also, so that the pivoting axis is in a thicker part of the worm and the torque here would account for the broad haptoral wing. The testicular zone is not involved in the torque and the 2–4 files are rather regular and compact (Fig. 12). There are 15–31 testes, ovoid or spheroidal, with one or two parovarian testes. The vas deferens is long and wide, arising from the median anterior testicular zone and extending forward as a zigzag duct to open into the base of the penis. The anterior extremity of the vas deferens, before it joins the penis, is straight, forming the ejaculatory duct; this has a posterior dilatation between the horns of the vaginae functioning as the seminal vesicle (Fig. 17); the penis is muscular, ventral, situated about 0.18–0.2 mm from the anterior end, and bearing a corona of 10 sharp hooks, but its tip lacks forceps spines. The atrium masculinus is unarmed and circular, with a muscular rim and a thick ring of radial muscle fibres but no projecting membranous collar (Figs. 16a and 16b).

The ovary takes the form of an inverted U with a long narrow proximal (outer) limb and a wide short distal (inner) limb, situated in the middle third of the body, in front of the testicular zone. The thin and narrow oviduct descends from the distal end of the ovary and opens into the fertilization chamber, through the well-developed, spindle-shaped ovijector (Fig. 17). The oötype is surrounded by closely packed Mehlis gland cells. The uterus ascends from the oötype to open into the unarmed uterine pore in front of the atrium masculinus. Eggs were seen in only one of the specimens.

The vitellaria extend from the intestinal bifurcation to almost the distal ends of the crura; they are not confluent across the median line, and their spherical follicles are 8–10 μ in diameter. The transverse vitelline ducts meet to form the median duct at the anterior quarter of the ovarian zone, as in *E. triaptella*, but here they are joined by the lateral vaginal ducts. The median vitelline duct is broad anteriorly and tapers posteriorly to open into the vitelline ampulla, which is feebly demarcated in most of the specimens. The genito-intestinal canal is well differentiated, arising from the oötype close to the ovijector, and running obliquely into the right crus.

The two dorsal vaginal pores are unarmed, one in each midlateral field in front of the ovary in the anterior part of the middle third of the body, well in front of the transverse vitelline ducts. The lateral vaginal ducts are packed with sperm cells and twisted in S-shaped sinuous ducts which run backward to unite with the transverse vitelline ducts near their junction with the median vitelline duct.

RELATIONSHIPS OF *Engrauliphila grex* GEN. ET SP. NOV.:

1. *Engrauliphila* has a haptor-body relation similar to that in *Engraulixenus*.
   i. The stouter body is provided with a somewhat thicker haptoral flange and the clamps have more muscular and longer stalks.
   ii. In comparable-sized worms, the haptor is more extensive, reaching into the ovarian zone, so that the zone of pivoting is in a thicker region and the resulting torque would account for the relatively more massive (metahaptoral) wing.
   iii. The length of the clamp row is more than 50% that of the relaxed worm.

2. The inhibited clamp row retains only two primary clamps in all specimens.
   i. The long clamp row bears 40–48 transversely elongated stalked clamps in close file.
   ii. The dorsal appendix on the spring is stout and V-shaped.
   iii. The ventral arm of the spring is broad, splayed, and bifurcate.
   iv. The braces do not have bent articular ends.

3. The two pairs of persistent anchors are of distinctive shape, both less curved than in *Engraulixenus* and entirely unlike those of *Gastrocotyle* and *Engraulicola*.

4. The penis head is devoid of forceps and a collar is lacking round the atrium.
   i. The corona consists of 10 sharp divergent spines, but no sigmoid spines.
   ii. The 15–31 testes are in 2–4 compact files, with 1 or 2 parovarial.
   iii. There is a vesicula seminalis in the preovarian zone.

5. The vaginae are paired and lie in midlateral fields on the dorsal side; there is no median vaginal duct, since they join the transverse vitelline ducts near their confluence, as in *Engrauliphila*; the vulvae are not supramarginal and are situated much nearer the ovary.
   i. The vulvae are less than an ovary length in front of the ovarian zone.
   ii. The transverse vitelline ducts are situated at the level of the anterior quarter of the ovarian zone.

6. The pharynx is elongated ovoid, and the oral pouches are spheroidal and much smaller.
   i. The mean diagonal of the latter is about 50% that of the pharynx.
   ii. The crura lack inner branches and there are no intercrural bridges at all.
   iii. The unequal ends of the crura are only slightly dilated.

The assemblage of differences in the generic criteria taken together are in sufficient contrast to those of *Engrauliphila* for *Engraulixenus* to be recognized as distinct. The specific name *grex* refers to the exceptionally high infestation rate on *Thrissocles dussumieri*.

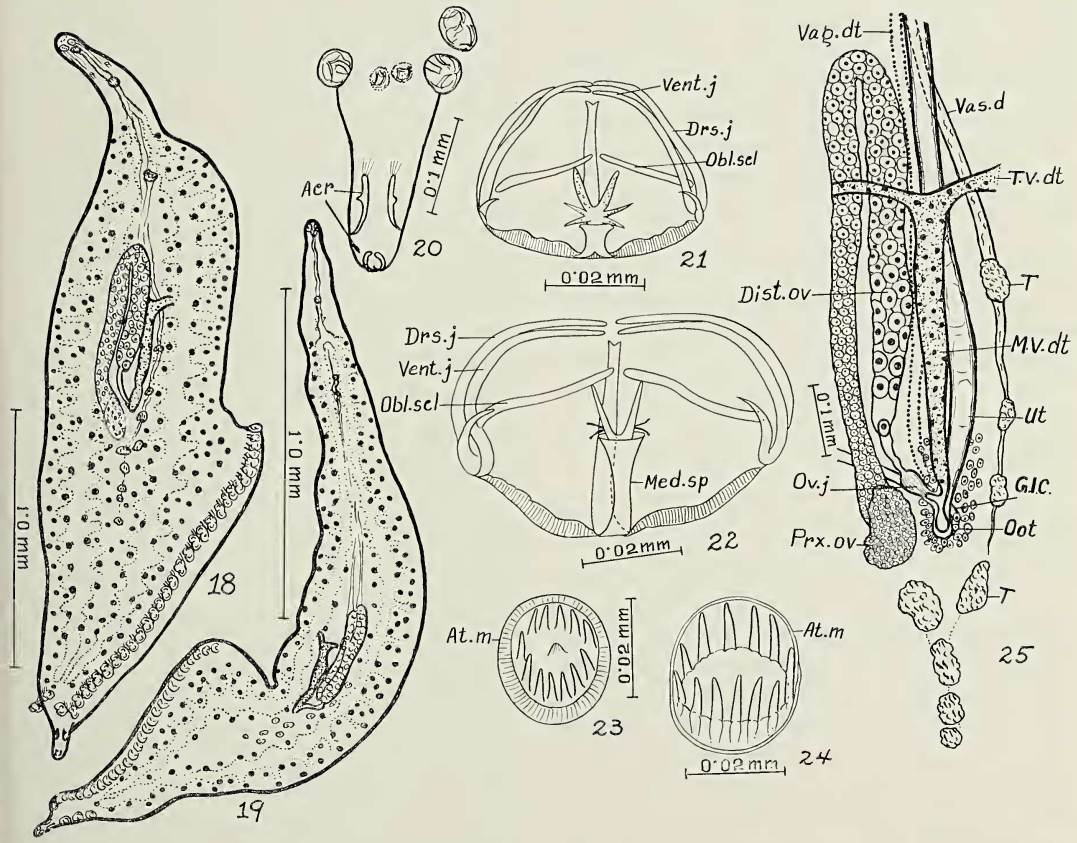
Engrauliscobina triaptella sp. nov.
Figs. 18–25

Specimens of this second species of *Engrauliscobina* Unnithan, 1967*b* were obtained from the gills of *Thrissocles dussumieri* (Val.) examined at Vizhinjom and Trivandrum on August 19, 1954 and October 5, 1955, respectively. Two fishes examined at Vizhinjom were infected by four individuals (two on each fish), while several of the *T. dussumieri* examined at Trivandrum were found to be parasitized by one specimen of *E. triaptella* along with a large number of *Engrauliphila grex*. Such multiple infection was not observed on the several *Thrissocles dussumieri* examined at Ayiramthengu on September 8, 1955, which were infected only by *Engrauliphila grex*.

The essential asymmetry of these worms is shown typically in one of the longer but somewhat contracted specimens (Fig. 18); a younger one is shown extended in Figure 19, in which the bulging of the shorter side is marked. The characteristic shape is triangular, as it is in the

genotype *Engrauliscobina thrissocles* (Tripathi). There is no demarcation of the haptoral region from the body proper, since the clamp row flanks the side of the body opposite the anterior region of the testicular zone or extends partly into the ovarian zone providing one of the shorter sides of the triangle. The length of these typical specimens is 2.4 and 2.9 mm, and their maximum width (between the gonad zones but excluding the haptoral wing) is 0.4 and 0.7 mm, respectively, giving a width-to-length ratio of 16.5%:24%—the latter being more typical. The worms are strongly flattened dorsoventrally and highly extensible and contractile; in extension they are able to flex the body over a wide arc based on the fixed haptor, the axis of pivoting being in the thickest and widest zone; the resulting stresses would account for the convexity on the short side above the long clamp row. The shape of the whole body is like that of a scraper (particularly so in the genotype); the handle of the scraper is here more abruptly demarcated, forming the neck which is about one-fifth the total length of the body axis, as it is in the genotype; and here again the body axis is bent at a small angle between the ovarian and testicular zones, even in the contracted specimen (cf. my Fig. 18 and Tripathi's [1959] Fig. 56*a*).

The subterminal mouth has scattered gland cells only on the anterior lip. The oral pouches are longitudinally ovoid, 24 × 20 μ, and have long muscle fibres extending posteriorly from their thick outer walls. The pharnyx is oval,



FIGS. 18–25. *Engrauliscobina triaptella* sp. nov. *18,* Complete worm, ventral view; *19,* another complete worm with three clamps in the short row; *20,* hind end of the haptor with the pair of incipient clamps of the worm with only two clamps in the short row; *21,* first clamp nearest the lappet on the short row, dorsal view; *22,* one of the middle clamps of the long row, dorsal view; *23,* male genital pore with the penis head; *24,* corona of spines of the male genital pore; *25,* oötype and ovarian region, ventral view.

thick-walled, and only slightly larger than the oral pouches, 24 × 40 μ, the mean diagonals of the pouches being as much as 70% that of the pharynx. The oesophagus is 0.16 mm long and unbranched, and bifurcates into the intestinal crura immediately behind the male genital pore. At the posterior end of the neck region, the crura have numerous complex outer branches and a few simple inner branches; they are particularly extensive on the side bearing the clamp row. The crural ends are close together near the tip of the body, but they are not confluent across the median line, nor were any intercrural bridges seen.

The haptor, represented by the unilateral clamp-bearing flange on the hindbody and including the lappet, is slightly less than half the total length of the slightly contracted worm (Fig. 18), but in the extended condition it is only 36%. The long clamp row (usually on the left) is 0.825–1.35 mm long, bearing 27–35 almost sessile clamps. The inhibited side of the haptor is represented in all specimens by 3 remnant clamps, and together they make a row only 0.10–0.12 mm long. Occasionally (as shown in Fig. 18), there may appear to be only 2 remnant clamps in the short row (usually the right side in my collections), but in Figure 20 it will be seen that the first two primary clamps are relatively minute and lie close together near the median line between the second pair of primary clamps—virtually the end clamp of each row. In most specimens the three clamps of the inhibited side are subequal and in a linear series, as in Figure 19.

The terminal lappet is short, narrow, and cylindrical, 0.82 × 0.25 mm–0.98 × 0.48 mm, armed with two pairs of symmetrically arranged anchors. The anterior anchors have their hooks only slightly sickle-shaped (one-quarter to one-third of a circle), with a knoblike spur at the top of the slender handle, which may be less than one-half the total length of the anchors (40 μ). The posterior anchors are almost ⊂-shaped, with a reflexed strongly rounded hook but a very short handle (total length 12–16 μ). Both pairs of anchors are similar to those figured by Tripathi (1959), but while the anterior pair is like those of *Engrauliphila* the posterior pair resembles only those of *Engraulicola micropharyngella.*

The clamps in the long row are 44 × 52 μ–35 × 75 μ, and in the short row 20 × 28 μ–30 × 48 μ. Thus, the primary clamps of both rows are smaller and only slightly wider than long, but those in the long row are graded as usual, the largest being on either side of the middle region, and more than twice as wide as long. The braces are situated across this longer diameter; they are nearly straight with bent ends lacking the bent articular facet, though they do meet medially near the level of the divergent V-like arms of the dorsal appendix. The ventral arm of the spring is very slender, with or without a very slight enlargement at its end, but this extremity is always with a minute notch, never truly bifurcated (see Figs. 21 and 22).

There are 9–12 irregularly oval testes, 60 × 75 μ–75 × 150 μ, arranged in two files and not in a single mass as depicted for the genotype. The row on the side opposite the clamps is completely postovarian, while that nearer the clamp row extends forward to the middle of the ovary along the outer edge of the median vitelline duct; these parovarian follicles were not found in *E. thrissocles.* The vas deferens originates from the anteriormost testes of the parovarian file, runs forward parallel to the uterus, and opens into a zigzag ejaculatory duct which in turn opens into the penis. No vesicula seminalis was seen. The muscular penis is small and conical, without forceps, and opens into the circular atrium masculinus, which is surrounded by a muscular ring 20–24 μ in diameter, situated at about 0.16–0.19 mm from the anterior end of the body. The penis itself bears around its widest diameter a corona of 12 sharp conical spines pointing vertically from the ventral surface; the spines are nearly straight. Figures 23 and 24, drawn from ventral and dorsal aspects, are intended to demonstrate the entire absence of forceps on the penis head.

The ovary is in the form of an elongated inverted ∪, with the distal (inner) arm wider and containing a number of large ova, and the proximal end slightly swollen and overlapped by the anterior testes of the postovarian file. The short and narrow oviduct expands slightly to form a muscular ovijector, before opening into the vitelline ampulla (Fig. 25). The wide median uterus arises from the outer margin of the fertilization chamber in the oötype, runs

forward parallel to the common vitelline duct, and opens into the unarmed uterine pore in front of the male genital pore. Two or three eggs with polar filaments were observed in most of the specimens, but usually were too collapsed for reliable measurements.

The vitellaria occupy wide lateral fields extending from the zone of intestinal bifurcation to the hind end of each crus; follicles are spherical, 20–25 μ in diameter, not confluent across the median line. The transverse vitelline ducts are broad and lie at the level of the anterior quarter of the ovary; the median vitelline duct is long and wide, and originates behind the anterior third of the ovary; it narrows as it passes backward, and it opens into the swollen vitelline ampulla in the oötype region (Fig. 25).

The single median dorsal vaginal pore is circular, 20 μ in diameter, unarmed, but surrounded by a group of small spherical gland cells. It is situated a short distance behind the intestinal bifurcation (midway between the male genital pore and the transverse vitelline ducts). It is in this zone that asymmetry is particularly striking: on the side of the clamp row (usually at the left) there is, at least in nonextended worms, a marked hump on the profile before the indentation at the base of the neck (Fig. 18), and a low furrow from the vulva on the dorsal side leads obliquely to the indentation. This is the anterior limit of the lateral branching of the crus and attendant vitellaria of that side. On the opposite side the profile is nearly straight from the neck zone to the lappet, and the vitellaria extend farther anteriorly along with short external crural branches to the bifurcation on that side. This notch opposite the vulva may facilitate a finer hold during copulation in these worms, where the torque from the oblique attachment must be considerable. The median narrow vaginal duct runs backward dorsal to the uterus, between the oviduct and the median vitelline duct, to open directly into the fertilization chamber. It is quite independent of the vitelline duct. The genito-intestinal canal originates from the base of the oötype, runs parallel to the ovijector, and opens into the intestinal crus.

Two ill-defined excretory pores, one on each margin, are noticeable, midway between the male genital pore and the pharynx.

RELATIONSHIPS OF *Engrauliscobina triaptella* SP. NOV.:

1. In the more or less contracted state, *E. triaptella* is a triangle with the long clamp row as its shortest side; the inhibited haptor side of the worm is only slightly convex. In the generally similar genotype, *E. thrissocles* (Tripathi, 1959), the body is a much narrower triangle; in both there is a narrow neck, about one-fifth of the total length. The haptoral row embraces more of the body in the genotype, including the hind region of the ovarian zone, but it is more restricted in *E. triaptella,* being barely included in the ovarian zone. Hence, the torque in the latter species is less, and the (meta-) haptoral wing is not so extensive, in order to balance these stresses, as it is in the genotype. A further consequence of the torque is visible in *E. triaptella* in the vaginal zone, marked by a hump on the profile on the attached side of the worm and an inhibition of lateral crural branches and vitellaria anterior to the hump and neckbase, the opposite side being unaffected. In fact, the asymmetry in this species is more marked than in any other gastrocotylid and approaches that in some Opisthogynidae and Protomicrocotylidae.

   i. The clamp flange is about 36%–48% of the total length in *E. triaptella* (the greater the contraction the greater the proportion, of course), while in the genotype it is about 50%.
   ii. The angle made by the haptoral axis with that of the body proper is about 45°, compared with nearly 60° in the genotype.
   iii. The body torque produces a permanent slight bend in the axis of the ovarian to the testicular zones.

2. There are remnant clamps on the inhibited side of the haptor, only 2 in the genotype, but 3 in *E. triaptella* (hence its name). The uninhibited row in mature worms bears at least 30 nearly sessile clamps.

   i. There are up to 35 clamps in the new species, but 40–42 in *E. thrissocles.*
   ii. The secondary clamps (but not the squarish primaries) are at least twice as wide as long in *E. triaptella.*
   iii. The ventral arm of the median spring is

slender and tapers to a minutely notched tip.

iv. The dorsal appendix on the spring is a simple V shape.

v. The braces are slender and nearly straight and lack the bent articular distal facet in *E. triaptella.* There is no description or figure of the secondary clamps for *E. thrissocles.*

3. The two pairs of persistent anchors on the lappet are of characteristic shape in both species. The genotype retains a pair of minute larval hooks at the tip of the lappet.

i. The anterior anchors are slender, with feebly curved hooks (about one-third to one-half a circle), and with a knoblike spur and the handle barely half or less of the total length (40 μ).

ii. The posterior anchors are ⊂-shaped or sharply reflexed simple hooks with negligible handles (root).

4. The penis head is absolutely devoid of forceps, the corona hooks are straight.

i. There are 10 penis hooks in *E. triaptella* but 12 in *E. thrissocles.*

ii. There are 9 to 12 irregularly shaped, rather large testes in two files, with some of the files (nearer the clamps) parovarial. In *E. thrissocles* there are perhaps no parovarial testes.

iii. There is no intercalary vesicula seminalis on the vas deferens.

5. The single median dorsal vagina leads to a median duct independent of the vitelline ducts.

i. The zone of the vulva is midway between the male genital pore and the ovary.

ii. The vitelline ducts are horizontally transverse at the first quarter of the ovarian zone.

6. The moderately ovoid pharynx is only about twice as long as the oral pouches.

i. The oral pouches' mean diameter is about 70% of that of the pharynx (about 56% in the genotype).

ii. The lateral crural branches are extensive in the haptoral wing, but there are no intercrural bridges and the crura extend without dilation to near the posterior tip of the body in both species.

The two species are closely related yet clearly distinct and occur on different species of *Thrissocles,* the genotype occurring in the northern Bay of Bengal (Puri) and *E. triaptella* in the South Arabian Sea and at two stations in southern Kerala.

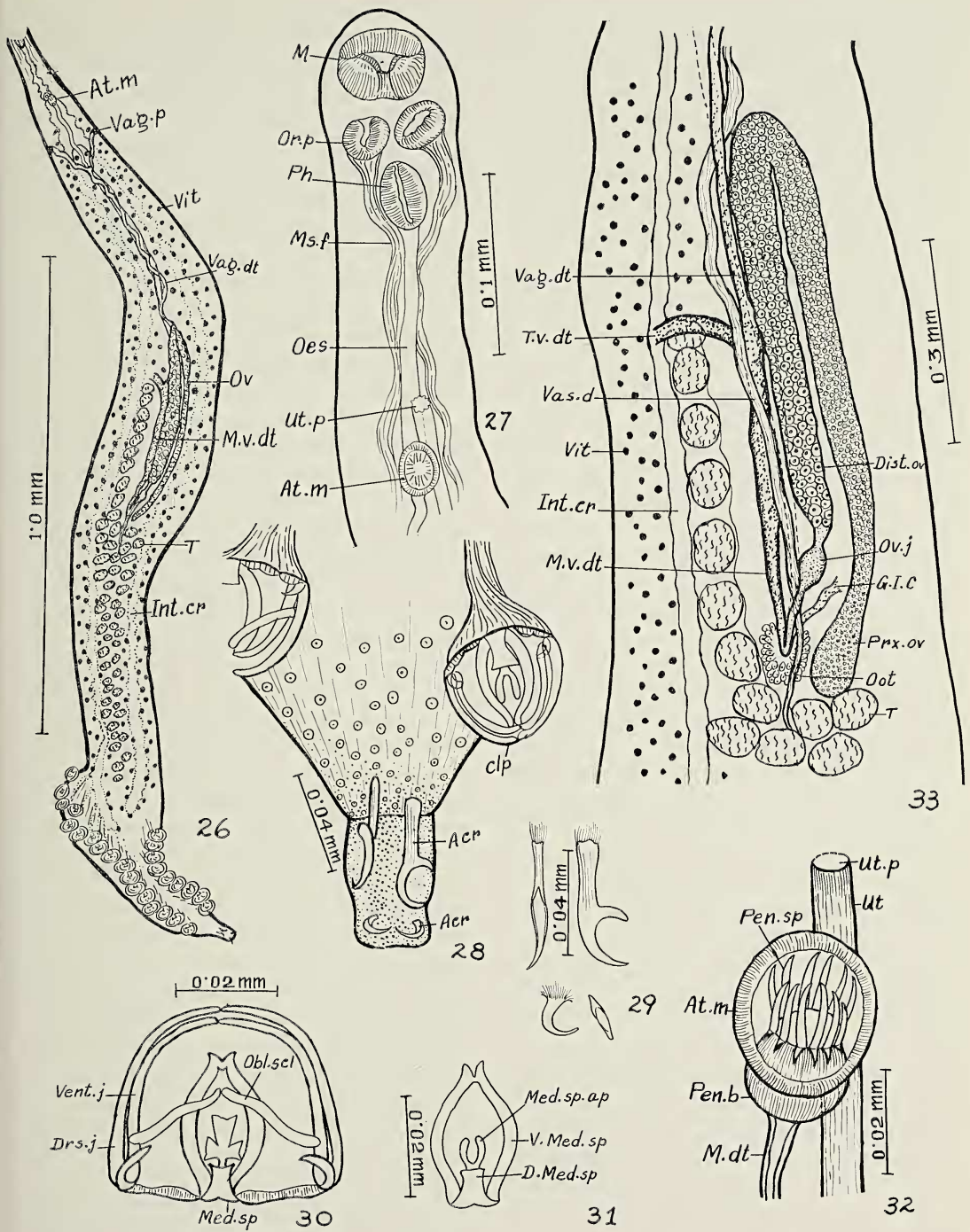
Pellonicola elongata gen. et sp. nov.

Figs. 26–33

Several specimens of this new gastrocotyline were obtained from the gills of *Pellona (Ilisha) brachysoma* (Blkr.) examined at Trivandrum in 1955. A single fish 17 cm long was examined on July 5, and 4 parasites were found on its outer gills; a single female fish 17 cm long, examined on August 27, had 4 parasites. From 5 fishes 18 cm in average length, examined on July 27, 14 specimens were obtained. The 4 specimens collected on July 5 proved to be the longest among the total of 22 specimens.

The long, narrow, ribbon-like body (2.25–4.5 mm long, maximum width 0.25–0.48 mm, or one-tenth its total length), tapers gently forward to a nearly straight neck little more than one-tenth of the total length and itself one-fifth to one-quarter as long as wide. The middle third of the body is expanded 25% to accommodate the ovarian zone and reaches its maximum at the proximal ovarian zone; behind this the testicular zone is almost straight-edged and is as wide as the preovarian zone (Fig. 26). The haptor is relatively far shorter than in any other gastrocotyline yet known, barely one-fifth the total length (0.525 × 0.15 mm–1.0 × 0.3 mm), one clamp row being twice as long as the other, with subsequal clamps ending in a short telescopic lappet.

The subterminal funnel-shaped mouth is surrounded by a highly muscular spherical-to-oval organ having a deep circular lip with a ventral notch, and a chamber measuring 45–50 μ. Behind it are the ovoid oral pouches, 20 × 28 μ–24 × 36 μ, and these have thick walls and long muscle fibres extending down the length of the neck (Fig. 27). The pharynx is a large ovoid structure, 34 × 38 μ–36 × 40 μ. The mean diagonal of the oral pouches is about 61–78%



FIGS. 26–33. *Pellonicola elongata* gen. et sp. nov. *26,* Complete worm, dorsal view; *27,* anterior region, dorsal view; *28,* terminal lappet with anchors; *29,* anchors; *30,* clamp, dorsal view; *31,* median spring of the clamp of another worm, dorsal view; *32,* male terminalia with the uterus, ventral view; *33,* middle of the body, dorsal view.

of that of the pharynx. The oesophagus is long, narrow, and unbranched, and bifurcates into the intestinal crura well behind the male pore. The crura have relatively few regular outer branches, extend backward to the level of the proximal end of the short row of clamps, and terminate independently, but close to each other, without inflations. The crus adjacent to the longer clamp row sends out wide oblique branches to each of the anterior clamps.

The haptor in *Pellonicola*, in contrast to that in all the previous genera, is distinct from the body proper and constitutes a posterior tail. Its right and left haptoral frills are parallel, but one is only half as long as the other: in my specimens, the left frill is always the longer, 0.45–0.93 mm; the right frill range is 0.225–0.456 mm and it bears 8–10 clamps, 36 × 20 μ–44 × 36 μ, while the left frill has 17–22 clamps, 36 × 24 μ–48 × 32 μ.

The terminal lappet apparently is unique in its telescopic arrangement and consists of an oblique plaque capable of being retracted as a whole into the hollow end of the haptor (Fig. 28); it is 60 × 28 μ–68 × 36 μ, and is armed with the usual two pairs of anchors (Figs. 28 and 29). The anterior pair is distinctively shaped like a sickle, 40–44 μ long, with the handle about equal in length to the hook, but the spur root is more than half as long as the handle and projects at right angles from it. The tip of the spur is slightly curved but does not actually pivot backward, as in *Engraulicola micropharyngella* (Fig. 3), which otherwise it most resembles in this series (particularly on account of its sickle hook, which is slightly more than a half circle, although the handle is more slender and relatively longer). The posterior anchors are bent in a deep ⊂-shape and their over-all length is only 16–20 μ with virtually no handle, as in *Engraulicola triaptella* (Fig. 20, compare with Fig. 29). The placing of the anchors is invariable; the anterior pair is always directed outward and the posterior pair inward, their hooks nearly touching, in all genera.

The clamps are, exceptionally, slightly longer than wide, but their structure is very different in detail from any of those previously described: the median spring is highly modified, the ventral arm being vase-shaped in outline and apparently split longitudinally, with each half bowed outward; the tip is bifurcated. The short arm of the median spring, which has radiating tendonous striae at its distal end, has an appendix which in some specimens is typically ∪-shaped (Fig. 31), but in others is shaped like half a Maltese cross (Fig. 30). The braces (oblique sclerites) are stout and slightly wavy, and, although their inner ends touch in the middle line, there is no sharp bend here to form the familiar articular facet. The dorsal arm of the ventral jaw sclerite is unusually small, often appearing as a mere knob at the region of articulation of the dorsal and ventral jaws (compare Figs. 28 and 30).

There are 34–52 testes arranged in 2–3 rather regular files. On the side of the uninhibited clamp row there is a single file of a few testes extending parovarially up to the level of the transverse vitelline duct on the left side (Fig. 33); the anterior testes are largest (48 × 68 μ), while the posterior ones are smaller (16 × 20 μ). The vas deferens is long and zigzag, arising from between the anterior testes and running forward; in front of the ovary it widens into a large vesicular duct to about the level of the lateral vaginae, behind the intestinal bifurcation. This part probably functions as a seminal vesicle. Thence the vas deferens continues forward, to open into the base of the penis. The muscular cuplike penis is armed equatorially with a corona of 10–12 recurved spines, 10–12 μ long (Fig. 32), but the penis head within is devoid of forceps. The median ventral atrium masculinus has a rim of radial muscle fibres and is situated at about 0.12–0.27 mm from the anterior end of the body, in front of the intestinal bifurcation.

As usual, the ovary is in the form of an inverted ∪ and is situated in the middle third of the body, slightly shifted to the right side; the proximal region is oval and lies immediately in front of the testicular zone on the right side; it is long and narrow, and the distal limb is short (two-thirds the length of the longer limb) and contains large ova, each 12–14 μ in diameter. The short and narrow oviduct descends from the distal end of the ovary and enlarges into a well-demarcated ovijector at about the middle of its length and thence continues backward to open into the median vitelline duct,

within the oötype region (Fig. 33). The wide median uterus, with cuticularized walls, ascends from the distal margin of the oötype, extends forward beyond the vaginal region, and opens into the unarmed, ventral, uterine pore, immediately in front of the male pore (atrium masculinus) (Fig. 32). In one of the specimens a collapsed egg, with a body 120 μ long, was observed at about the middle of the uterus.

The vitellaria extend from behind the zone of the male terminalia to the anterior level of the short row of clamps, surrounding the crura and their branches but not confluent across the median line at the hind end; the vitelline follicles are spherical, 14–16 μ in diameter. The transverse vitelline ducts are slightly oblique and are situated near the posterior end of the anterior third of the ovarian zone; at their confluence they receive the median vaginal canal. The median vitelline duct extends backward parallel to the ovary and opens into the vitelline ampulla. The genito-intestinal canal is very narrow, irregularly wavy, and arises from the oötype. It runs obliquely forward to open into the right intestinal crus, near the proximal limb of the ovary.

The vaginal pores are unarmed, just supramarginal on each side of the body at about 0.25–0.52 mm from the anterior end, with the right pore usually slightly anterior to the left. The two vaginal ducts from the base of the lateral vaginal pores unite obliquely as a V across the median line to form a long median zigzag vaginal duct which runs backward, dorsal to the uterus, and opens into the median vitelline duct at the junction of the transverse vitelline ducts, hence *indirectly* to the oötype region. In most of the specimens traces of vitelline matter were observed extending forward beyond the level of transverse vitelline ducts, into the median vaginal duct. Spindle-shaped eggs, with a filament at each pole, were seen in worms 4.5 mm long.

RELATIONSHIPS OF *Pellonicola elongata* GEN. ET SP. NOV.:

1. The elongated ribbon-like body with the distinct but short caudal haptor is outstanding in Gastrocotylinae. The body proper is free from the attachment zone, so the zone of pivoting in the extreme feeding attitudes is behind the testicular zone; but, because of the inequality of the attachment basis, the stresses will be slightly greater on one side than on the other, and so the profile in contracted worms is not as symmetrical as in *Microcotyle*, for instance. This slight asymmetry is most obvious in the vaginal zone at the neckbase, as it is in the most asymmetrical species of *Engrauliscobina*.

   i. The body axis makes an angle of up to 60° with the haptor axis.
   ii. The ratio of body width to length is only 1:10, and of haptor to body length about 1:5.

2. The unilateral inhibition is far less than that in any other genus of the asymmetrical gastrocotylines. In this respect it is comparable with *Scomberocotyle* Hargis, 1956, but in that genus a metahaptoral wing, or a secondary stimulation of the secondary clamp replication, accounts for the larger number of clamps on one side (Unnithan, 1967*b*). It is possible that further observation on *P. elongata* may show that a similar growth relation exists here and that the anterior moiety of the long clamp row does represent a metahaptor, the posterior moiety being the euhaptor with regular paired clamps in the opposite row. If this is so, the formative region for the long row would be near its middle, and that of the short row at its anterior limit, as is usual for the euhaptor.

   i. The long row has a total of 17–22 clamps, while the shorter has 8–10.
   ii. All clamps are slightly longer than wide. Perhaps this is a generic character.
   iii. The ventral arm of the median spring is of a unique vase shape and is split and bowed, joining distally in a very short bifurcation.
   iv. The appendix on the short dorsal arm is sometimes cruciform, indicating an incipient cuticularization of the lateral ligaments.
   v. The dorsal arms of the ventral jaw rami are remarkably reduced.
   vi. The braces across the middle of the capsule are stout but lack distally bent articular facets.

3. Two pairs of persistent anchors are present on a telescopic lappet. Anterior anchors are

sickle-shaped, at least half a circle, with a nearly equal handle and a curved (not bent) spur.

i. Anterior anchors 40–44 μ, posterior anchors 16–20 μ bent in a deep ⊂-shape.

4. No additional sclerites are formed within the penis corona.

i. 10–12 curved penis hooks, and atrium well in front of intestinal bifurcation.
ii. 34–52 testes in 3 compact files with 6–8 parovarian testes.
iii. Intercalary vesicula seminalis anterior to ovarian zone.

5. There are two paired lateral vaginae with the vulvae supramarginal, as they are in *Engraulixenus*, but very far forward (one-fifth of distance from male pore to anterior border of ovary). The lateral ducts run obliquely back in a Y, to form a median vaginal duct (unusual with paired vaginae) which does not run directly to the oötype, but is confluent with the median vitelline duct.

i. The horizontal transverse vitelline ducts are at the level of the mid third of the ovarian zone, which is rather more posterior than in related species.

6. The ovoid pharynx is not particularly long (as it is in *Engraulixenus* and *Engrauliphila*), but the oral pouches are more powerful than in other genera.

i. The mean diagonal of the oral pouches is 66–78% of that of the pharynx in *P. elongata*.
ii. There are distinct simple branches of the right crus to each of the more anterior (unpaired) clamps of the long row.
iii. The crura are nearly equal and extend to the body tip without dilatations.

7. There are no intercrural bridges, but there is an exceptional circumoral, sucker-like, circular lip in *Pellonicola* that is not present in allied genera.

The above characters show that *Pellonicola* is a somewhat aberrant gastrocotyline, and that it is the first ever found on a member of the Clupeidae.

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